Seasonal, successional, and vertical segregation in a Maryland ant community

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Ecological segregation was studied in a diverse ant community within the coastal plain province of Maryland, USA. Distributional data were obtained from year-round samples of species associated with the litter and low arboreal strata in three successional sites. Of 52 species which were encountered, 19 occurred commonly enough for quantitative niche analysis. Most local ant species are trophic generalists, but are specialized with respect to major habitat (e.g., old-field vs. forest). Additional differentiation is achieved by vertical segregation of foraging microhabitat and by dispersion of seasonal activity modes. Formal analysis of the components of diversity indicates that the independent contributions of three resource dimensions (successional habitat, vertical microhabitat, and seasonal activity) together account for about half of the observed total community diversity, while within-microhabitat overlap contributes an additional 37%. The remaining 13% of the observed community diversity is due to 2-way and 3-way interactions (i.e., redundancy) among the three resource axes. Niche breadth is shown to be correlated with overall abundance across all habitats, but local abundance within favored habitat-microhabitat combinations is largely independent of niche breadth.

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Исследовали экологическую сегрегацию в разновидовом сообществе муравьев на прибрежной равнинной территории Мэриленда (США). Данные по распределению получены в результате круглогодичных сборов видов, связанных с подстилкой и нижними ярусами древесной растительности в 3-х сукцессионных стациях. Из 52 собранных видов 19 встречались достаточно часто для проведения количественного анализа их распределения между разными экологическими нишами. Наиболее локальные виды муравьев – всеядные, однако, они специализированы к основному типу биотопа (например, к залежам в противоположность лесным стациям). Дальнейшая дифференциация достигается вертикальной сегрегацией фуражировочных микробиотопов и сезонной дисперсией активности. Формальный анализ компонентов разнообразия показал, что независимые данные трех параметров ресурсов (сукцессионный биотоп, вертикальный микробиотоп и характер сезонной активности) дают вместе примерно половину общего разнообразия сообщества, а перекрывание внутри биотопа – дополнительно 37%. Остальные 13% разнообразия создаются засчет 2 – и 3-канальных взаимодействий (т.е. избыточности) между 3-мя осями ресурсов. Показано, что ширина ниши коррелирует с общим обилием во всех биотопах, но локальное обилие в пределах предпочитаемых комбинаций биотоп-микробиотоп в целом независит от ширины ниши.

1. Introduction

There are comparatively few modern studies of the diverse ant communities associated with the deciduous forest region of eastern North America, though considerable information has been gathered for some ant species in southern Canada (e.g., Letendre et al. 1971, Letendre and Pilon 1972, Sanders 1972) and the midwestern USA (e.g., Headley 1941, 1949, 1953, Talbot 1934–1975). Only Goldstein's (1973, 1975) study of ant communities on small islands and the adjacent mainland on the New England coast, Culver's (1974) comparison of species-packing in Puerto Rican and West Virginian ant communities, and Feener's (1978) examination of litter-foraging ants at a Texas site have applied quantitative community analysis to studies of the rich eastern ant fauna.

An earlier paper (Lynch et al. 1980) considered seasonal and diurnal activity patterns in a guild of surface-foraging forest ants in Maryland, USA, based on year-round observations of ants attracted to baits. The present paper describes seasonal, successional, and vertical modes of segregation in a series of ant communities from the same region in the Maryland coastal plain. The goals of this study were to quantify spatial and temporal distribution patterns for the major ant species, to assess the relative contributions of succesional macrohabitat, vertical microhabitat, and seasonality to total species diversity, and to document patterns of niche breadth and dominance.

2. Methods

2.1. Study site

Three study sites were selected as representative of distinct stages of secondary plant succession following cessation of human disturbance. Site A was a brushy old-field that had been abandoned from agriculture for 5–6 yr. Site B had been abandoned for 30–35 yr, and supported a dense growth of young deciduous trees. Site C had last been farmed approximately 110–125 yr prior to the study, and supported a rich maturing deciduous forest. At each site a 2 ha plot was surveyed on a 20 m grid system, and nodal points were assigned coordinate numbers. Ten points were randomly selected each month as sampling loci; a given point was not sampled in successive months.

Field work was conducted at the Smithsonian Institution's Chesapeake Bay Center for Environmental Studies, a 900$^+$ ha reserve that borders Chesapeake Bay, approximately 10 km SSW Annapolis, Anne Arundel County, Maryland, USA (38°53'N, 76°33'W). Long-term weather data for Annapolis indicate a humid continental climate, with warm summers (mean July temperature = 25.3°C), mild winters (mean January temperature = 2.2°C), and an average annual rainfall of 108 cm. The gently rolling terrain is typical of the mid-

dle Atlantic Coastal Plain in supporting substantial areas of forest as well as a considerable proportion of agricultural land and abandoned fields. The most recent available vegetation map (Brush et al. 1980) places the study site within the Tulip Poplar (= Yellow Poplar) assemblage, a northern formation, rather than the southern Pine-Hardwood assemblage. This is a reasonable assignment in view of the virtual absence from local woodlands of Loblolly Pine *Pinus taeda* L., a characteristic indicator species of the Pine-Hardwood assemblage.

Data concerning the vegetation on the study sites were obtained from personal observation and from unpublished studies by D. F. Whigham, D. Higman, B. Simpson, and P. Opler. Plant names follow Radford et al. (1968).

Quantitative surveys of five randomly located 10 × 10 m plots at Stevens Field (Site A), indicated the following understory plants to be dominants in 1975: Broomsedge *Andropogon* spp., Fall Red Top Grass *Agrostis stolonifera* L., Goldenrod *Solidago* spp., Blackberry *Rubus* spp., Trumpetvine *Campsis radicans* L., Star-of-Bethlehem *Ornithogalum umbellatum* L., Ragweed *Ambrosia artemisifolia* L., Queen Anne's Lace *Daucus carota* L., *Lespedeza* spp., Beggar's Tick *Desmodium glabellum* Michaux, Partridge Pea *Cassia fasciculata* Michaux, and *Eupatorium* spp. Large sections of the field were dominated by clones of Japanese Honeysuckle *Lonicera japonica* Thunberg, a viny exotic. Small trees (height up to 2 m) were common, particularly near the forested margins of the field, where young sweetgum *Liquidambar styraciflua* L. formed dense stands. Other characteristic pioneering trees included Tulip Poplar *Liriodendron tulipifera* L., Red Maple *Acer rubrum* L., Sassafrass *Sassafras albidum* Nuttal, Virginia Pine *Pinus virginiana* Miller, Red Cedar *Juniperus virginiana* L. and Flowering Dogwood *Cornus florida* L.

The intermediate successional site (Site B) supported a dense growth of young hardwoods strongly dominated by Sweetgum, with lesser numbers of Tulip Poplar, Black Cherry, Sassafrass, Red Maple and Persimmon *Diospyros virginiana* L. The understory was dominated by Poison Ivy *Rhus radicans* L., which occurred in every one of 50 randomly placed 1 m^2 plots, and by Japanese Honeysuckle. Other abundant understory plants were wild onion *Allium vineale* L., Trumpet Vine, Indian Strawberry *Cuchesnea indica* Andrz., Bedstraw *Galium circaezans* Michaux, Avena *Geum canadense* Jacquin, Rattlesnake Fern *Botrichium virginianum* L., and Ebony Spleenwort *Asplenium platyneuron* L.

Site C was located within a large (ca. 50 ha) stand of maturing hardwood forest. In order of decreasing abundance, the main canopy tree species were Tulip Poplar, American Beech *Fagus grandifolia* Ehrhart, Pignut Hickory *Carya glabra* Miller, Mockernut Hickory *C. tomentosa* Poiret, Sweetgum, White Oak *Quercus alba* L., Black Oak *Q. velutina* Lam., Dogwood, American

Hornbeam *Carpinus caroliniana* Walter, Southern Red Oak *Q. falcata* Michaux, and Red Hickory *C. ovalis* Wang. The understory was dominated by Flowering Dogwood, American Hornbeam, American Holly *Ilex opaca* Aiten, Mountain Laurel *Kalmia latifolia* L., Spicebush *Lindera benzoin* L., False Solomon's-Seal *Smilacina racemosa* Dest., Bellwort *Arisaema triphyllum* L., Downy Rattlesnake Plantain *Goodyera pubescens* Willd., Puttyroot *Aplectrum hyemale* Muhl. ex Willd., Spring Beauty *Claytonia virginica* L., Mayapple *Podophyllum peltatum* L., Toothwort *Dentaria laciniata* Muhl. Beggar's Tick, Violet *Viola* sp., and Bedstraw.

2.2. Sweep samples

Sweep samples of the understory vegetation (height: 0.5–1.5 m) were taken at 3–4 wk intervals between 15 May 1975 and 2 July 1976. The three sites were sampled simultaneously by the author and two assistants, eliminating inter-site variability related to time of day. All sampling was conducted between 1000 and 1300 hours on days when no measurable precipitation had occurred within the previous 24-h period, thereby reducing variation due to short-term weather differences. Collectors were assigned randomly to the three study sites, so individual differences in sweeping technique should not have influenced the overall results.

At each randomly determined sampling point a standard heavy-duty beating net (hoop diameter 38 cm) was used to take 50 vigorous sweeps through the vegetation while walking an "x" shaped path centered at the point. The distance between sweeps was standardized at approximately 1 m, so each 50-sweep sample extended in four directions 12–13 m from the central point. Ten such 50-sweep sets from each of the three sites constituted a day's sample.

Net contents were emptied into separate plastic bags, and arthropods were later killed either by freezing them or by injecting ethyl acetate into the bag. Invertebrates were carefully sorted from associated plant debris and were stored in 70% ethanol for subsequent indentification (J. F. Lynch and W. G. Steiner unpubl.). Ants were sorted and identified by the author, with verifications by R. R. Snelling, Dept of Entomology, Natural History Museum of Los Angeles County.

2.3. Litter samples

Litter samples were collected at 3–4 wk intervals between July 1975 and June 1976 at the same three sites where sweep sampling was conducted. At each of ten randomly selected grid coordinates, a 0.1 m² sampling frame was tossed to the ground within 2 m of the nodal point. The only conscious deviation from randomness was an attempt to avoid logs and areas of bare soil. Any live vegetation within the sampling frame was clipped and discarded, and litter was quickly scooped into a sealable plastic bag. Ten samples were collected from

each site by the same worker in one morning, and were immediately processed in 30 large (diam. = 0.5 m) Berlese extractors equipped with 60 W drying bulbs. Litter samples remained in the extractors for at least 14 d, though few invertebrates were observed to accumulate in the collecting jars after the first 4–6 d. That ants were efficiently removed from the litter by this procedure is indicated by the fact that entire colonies (including brood and reproductives) of even the most delicate species (e.g., *Brachymyrmex depilis* Emery) were commonly extracted. Sorting and identification procedures were as described for the sweep samples.

2.4. Numerical analysis

2.4.1. Units of occurrence

A problem in statistically analyzing the occurrence data stems from the clumped distribution of individual ants. Large numbers of conspecific ants in a small area do not represent independent occurrences, and I followed Levins et al. (1973) in using the occurrence of a species, rather than the number of individuals, as the basic unit of abundance in the litter samples. Because conspecific ants in a given 0.1 m² area are likely to belong to the same colony, presence-absence data should be approximately equivalent to colony counts in such samples.

The situation was somewhat different for the sweep samples, which encompassed sufficient habitat (50 linear meters) to include workers from many different colonies of a given species. Still, each worker ant taken in a series of 50 sweeps is not an independent sample, for the foragers from a given colony will tend to be aggregated. Abundance of ants in sweep samples was assessed both as the number of species occurrences per set of 50 sweeps (i.e., presence-absence), and as the number of individuals per 50 sweeps. The "true" number of independent sampling entities (i.e., colonies) presumably lies somewhere between these two extremes.

Patterns of aggregation of ants within samples were quantified using Lloyd's (1967) indices of mean crowding and patchiness. These indices were derived by Lloyd from probability models that assume free-moving, non-colonial organisms, and computation of their standard errors requires assumption of random occurrence of individuals in quadrats. However, crowding and patchiness are useful descriptors of clumping even for sessile or colonial organisms.

2.4.2. Diversity and niche breadth statistics

The total diversity of any collection or community can be factored into components in a manner analogous to analysis of variance, but most previous workers have used hierarchical, non-interactive models in computing diversity components. Examples of such studies include community analyses of *Drosophila* (Levins 1968, Shorrocks 1975) and ants (Culver 1974, Feener 1978,

Levins et al. 1973, Pressick 1972, Pressick and Herbst 1973). As noted by Levins et al. (1973), habitat-microhabitat variables cannot be assumed to be mutually independent, and in the absence of a method for calculating interaction terms, the resolution of total diversity into its components is incomplete.

Alatalo and Alatalo (1977) described a method for calculating interactions among the variables in computations of diversity components, and give reasons for preferring the exponential form of the Shannon-Wiener diversity index over the more familiar untransformed version (H') as a measure of diversity (see also Hill 1973, Peet 1974):

$$EXP(H') = \ln^{-1}(-\Sigma\ P_i \ln P_i)$$

where P_i is the proportion of the ith species in the community. If presence-absence data are used, then for a given litter or sweep sample, EXP(H') is simply the number of species present.

If the total diversity of an ant community is considered to result from seasonal staggering of species (component A), interspecific differences in specialization on major successional habitat (component B), and vertical stratification of species within a given habitat (component C), together with a residual mean diversity resulting from species co-occurring in individual samples, we can write the following expression:

$$D \ldots = \bar{D} \ldots + V_{A/BC} + V_{B/AC} + V_{C/AB} +$$
$$R_{A\times B/C} + R_{A\times C/B} + R_{B\times C/A} + R_{A\times B\times C}$$

where $D \ldots$ = total community diversity,

$\bar{D} \ldots$ = mean diversity within habitat, vertical stratum, and season,

$V_{A/BC}$, $V_{B/AC}$, and $V_{C/AB}$ = independent diversity components due to variation in season, successional habitat, and vertical stratification,

$R_{A\times B/C}$, $R_{B\times C/A}$, $R_{A\times C/B}$ = diversity components due to non-independent variation (i.e., correlations) between each possible pair of niche components, and

$R_{A\times B\times C}$ = three-way interaction among niche components.

The interaction terms (R's) measure the degree of redundancy between niche axes. In principle, this analysis could be extended to include an indefinitely large number of additional niche dimensions, but because the number of interaction terms increases geometrically with the number of dimensions, both computation and interpretation become unwieldy for more than 3 axes. Computational formulas are given by Alatalo and Alatalo (1977), who analyzed only hypothetical data in their paper.

The exponential form of the Shannon-Wiener statistic was also used in niche breadth calculations. Computations were based on the mean number of species occurrences per ten samples within each of the 54 (= 9

seasonal intervals ×3 major habitats ×2 vertical strata) possible "resource states" (Colwell and Futuyma 1971). EXP(H') is thus equivalent to the effective number of resource states utilized and is maximized (EXP(H') = 54) when a species occurs with equal frequency at all seasons, in all successional habitats, and in both the litter and low arboreal strata. Conversely, EXP(H') is minimized (= 1) where a species occurs only at one time of year, in one successional habitat, and in one vertical stratum.

Interspecific comparisons of niche breadth are complicated by differences in species abundances. Rare species may appear to have narrow niches due simply to sampling error. Indeed, a species that is sampled only once can only have the minimum niche breadth, whatever its actual range of activity and tolerance might be. On the other hand, species that are locally abundant may or may not have broad niches, depending on their patterns of resource utilization. Computed niche breadths are useful indicators of ecological dispersion for such species, and I restricted the niche analysis to the 19 species that occurred at least 15 times in either the sweep samples or the litter samples. These accounted for nearly 90% of the individual ants collected (Tab. 1).

3. Results

3.1. The ant fauna

3.1.1. General

Some 60 ant species have been collected at CBCES (Lynch unpubl.), of which 52 were encountered in the present study. Eight of 52 (15.4%) species were collected only once, and several others were encountered fewer than ten times. The sampling methods of the present study are not meaningful for these uncommon to rare species, and they are omitted from the following analysis.

3.1.2. The litter fauna

The 450 litter samples yielded 4979 ants that represented 39 species (Tab. 1). The 15 species that occurred in 10 or more samples accounted for 88.0% of the 693 species occurrences, and 88.2% of the individual ants collected.

The Spearmann Rank correlation coefficient for relative abundance of individuals vs. relative frequency of occurrence is not significant for the 15 most abundant species ($r_s = 0.41$; $P > 0.05$), due to large interspecific differences in the number of individuals per occurrence. As an example, *A. pallipes* and *M. minimum* occurred in about the same number of litter samples (15 and 14), but the mean number of ants per occurrence was over 30 times higher in the latter species. This does not necessarily imply corresponding differences in the density of foraging workers, for most of the larger collec-

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Tab. 1. Successional habitat and vertical microhabitat occurrences for the 19 ant species encountered at least 15 times in the present study. Thirty-two additional species* were encountered less frequently. The maximum possible number of occurrences per habitat is 150 for the litter samples and 170 for the sweep samples. Site A was a 5–6 yr old abandoned field; Site B was a 35 yr old woodland; Site C was a 100+ yr old hardwood forest.

	Litter samples			Sweep samples		
	Site A	Site B	Site C	Site A	Site B	Site C
Subfamily Ponerinae						
Amblyopone pallipes			15			
Ponera pennsylvanica	22	30	36			
Subfamily Myrmicinae						
Aphaenogaster rudis	11	26	45		1	3
Crematogaster cerasi				12	1	8
C. clara				4	22	1
C. pilosa			40			
Leptothorax ambiguus	22	1		24		
L. curvispinosus	1	42	16	1	99	69
Monomorium minimum	14			86	1	2
Myrmecina americana		15	46			
Myrmica americana	8			26		
M. punctiventris			8		7	12
Smithistruma ohioensis		15	7			
Stenamma impar		9	36			
Subfamily Dolichoderinae						
Tapinoma sessile	14	4	1	44	50	4
Subfamily Formicinae						
Camponotus subbarbatus	2	2	1	25	57	
Formica pallidefulva	3			63		2
Lasius alienus	6	19	11	23	48	46
Paratrechina melanderi	2	42	38	7	64	70
Subtotal (19 species): *	105 (70.0%)	205 (94.5%)	300 (90.1%)	315 (88.7%)	350 (95.9%)	217 (77.0%)
Σ remaining 32 spp:	45 (30.0%)	12 (5.5%)	33 (9.9%)	40 (11.3%)	15 (4.1%)	65 (23.0%)
Total:	150 (100.0%)	217 (100.0%)	333 (100.0%)	355 (100.0%)	365 (100.0%)	282 (100.0%)

* Other species: Ponerinae – Hypoponera trigona, Proceratium pergandei; Myrmicinae – Aphaenogaster fulva, A. tennesseensis, A. treatae, Crematogaster lineolata, Harpagoxenus americanus, Leptothorax longispinosus, L. schaumi, Pheidole bicarinata, Ph. dentata, Ph. davisii, Solenopsis molesta, Stenamma diecki, Smithistruma clypeata, S. dietrichi, S. ornata, S. rostrata, Tetramorium caespitum; Dolichoderinae – Dolichoderus pustulatus, Iridomyrmex pruinosum; Formicinae – Acanthomyops claviger, Brachymyrmex depilis, Camponotus americanus, C. castaneus, C. ferrugineus, C. nearcticus, Formica integra, F. schaufussi, F. subsericea, Lasius meoniger, Prenolepis imparis.

tions of ants in litter samples represented nest fragments, rather than foragers (Tab. 4).

The 15 common species exhibit a wide range in the patchiness and crowding of their distributions. Although the two measures tend to be correlated (Tab. 2), considerable independent variation is possible. Thus, Solenopsis molesta, Leptothorax ambiguus, and Leptothorax curvispinosus all have similar indices of patchiness (m*/m = 11–14), but crowding (*) ranges from 6.6 in S. molesta to 44.8 in L. curvispinosus. Species with high crowding values (m* > 20) tend to forage on the surface or in the arboreal stratum, but often they temporarily locate their sizeable colonies in the litter zone. Conversely, species with low crowding values (e.g., Amblyopone pallipes, Myrmecina americana, Ponera pennsylvanica, Solenopsis molesta, Smithistruma ohioensis, Stenamma impar) forage mainly in the litter

or soil, and often place their generally small colonies below the litter in the soil zone (Lynch unpubl.).

Habitat associations of the 15 commonest litter species can be summarized in a triangular diagram (Fig. 1), with iso-diversity lines superimposed. The exponential form of the Shannon-Wiener function $(EXP(H') = EXP(-\Sigma P_i \ln P_i))$ is used to express the diversity of habitat utilization, where P_i = the relative frequency of occurrence of a given species in the ith major habitat category. A species with $EXP(H') = 3$ is a perfect habitat generalist, whereas the minimum value $(EXP(H') = 1)$ occurs when a species is restricted to one habitat. Five species (A. pallipes, C. pilosa, M. minimum, S. molesta, B. depilis) were encountered in one one of the three successional habitats, and may be considered habitat specialists. Three species (P. pennsylvanica, A. rudis, L. alienus) occurred in all three

Tab. 2. Patchiness and "mean crowding" (Lloyd 1967) for the 15 commonest ant species in the litter collections (A) and sweep samples (B). Calculations are based on occurrences in the major habitat for each species during the April–October activity season (N = 90 litter samples, 100 sweep samples). n = number of occurrences; m = mean number of individuals per sample; d = mean number of individuals per occurrence; S_x^2 = variance in number of individuals per collection; m* = mean crowding = $S_x^2/(m-1)$; P = patchiness = m*/m. Statistics computed only for sample site where species was most abundant.

| Species	Site	n	m	d	S^2	m*	P
A. Litter samples							
Amblyopone pallipes	C	11	0.13	1.09	0.14	0.18	1.34
Ponera pennsylvanica	C	33	1.34	3.67	9.71	7.57	5.63
Aphaenogaster rudis	C	41	2.50	5.49	6.41	17.95	7.18
Crematogaster pilosa	C	34	0.74	1.97	1.58	1.87	2.52
Leptothorax curvispinosus	B	29	3.02	9.38	129.39	44.84	14.84
Leptothorax ambiguus	A	18	1.88	9.39	39.32	21.82	11.62
Monomorium minimum	A	14	6.27	40.78	3165.82	509.81	81.25
Myrmecina americana	C	40	0.83	1.88	1.40	1.51	1.81
Solenopsis molesta	A	12	0.50	3.75	3.56	6.61	13.22
Stennamma impar	C	30	0.77	2.30	2.81	3.43	4.48
Smithistruma ohioensis	B	15	0.52	3.13	2.79	4.87	9.32
Tapinoma sessile	A	14	1.31	8.43	69.18	53.08	40.48
Brachymyrmex depilis	C	10	1.68	14.60	63.48	38.51	22.95
Lasius alienus	B	19	3.56	16.84	329.69	35.28	26.80
Paratrechina melanderi	B	34	5.37	14.20	205.88	42.73	7.96
B. Sweep samples							
Crematogaster clara	B	21	1.44	6.86	92.00	65.02	45.15
Crematogaster cerasi	A	18	0.62	3.44	2.84	6.21	10.01
Leptothorax curvispinosus	B	83	13.28	16.00	373.44	40.40	3.04
Leptothorax ambiguus	A	26	0.47	1.081	1.08	1.77	3.76
Monomorium minimum	A	80	24.77	30.96	2304.43	116.84	4.72
Myrmica americana	A	26	0.82	3.15	5.38	6.38	7.78
Myrmica punctiventris	C	9	0.21	2.33	0.79	4.99	23.76
Dolichoderus pustulatus	A	12	0.22	1.83	0.52	1.57	7.13
Tapinoma sessile	B	48	1.99	4.14	15.32	8.69	4.37
Camponotus subbarbatus	B	54	1.11	2.06	2.34	2.22	2.00
Formica pallidefulva	A	60	4.83	8.05	72.00	18.74	3.88
Lasius alienus	B	40	2.48	6.20	20.68	9.82	3.96
Lasius neoniger	A	10	0.14	1.40	0.26	1.02	7.28
Paratrechina melanderi	C	70	4.42	6.31	44.29	13.44	3.04
Prenolepis imparis	C	10	0.28	2.80	1.31	3.98	14.20
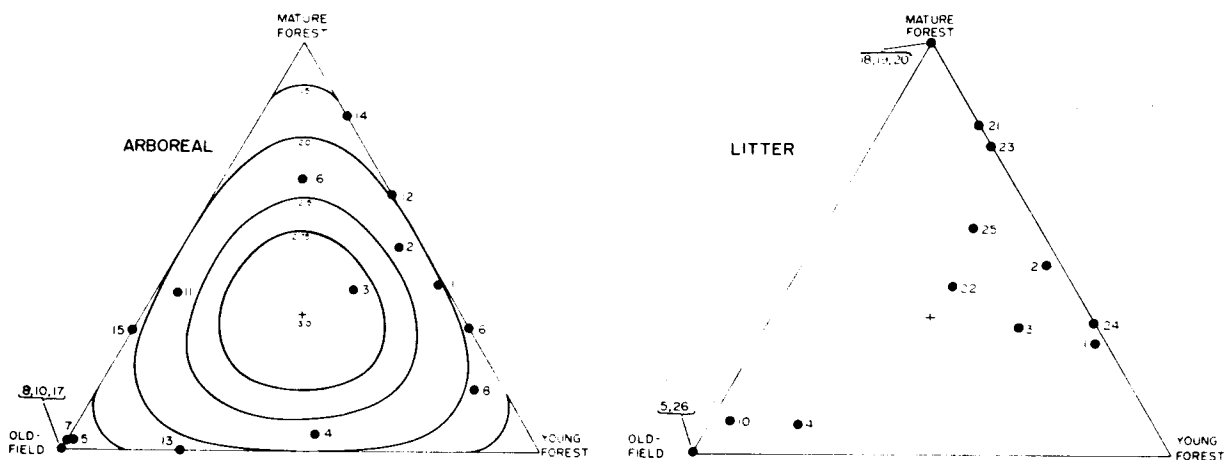
Fig. 1. Patterns of habitat specialization in arboreal (left) and litter-dwelling (right) ant species, based on sweep samples and litter samples, respectively. Extreme specialists plot at corners of triangular diagrams, complete generalists at the center. Iso-diversity contours indicated on one figure. Species: 1 – L. curvispinosus; 2 – P. melanderi; 3 – L. alienus; 4 – T. sessile; 5 – M. minimum; 6 – C. subbarbatus; 7 – F. pallidefulva; 8 – C. clara; 9 – Myrmica americana; 10 – L. ambiguus; 11 – C. cerasi; 12 – M. punctiventris; 13 – D. pustulatus; 14 – P. imparis; 15 – C. lineolata; 16 – F. subsericea; 17 – L. neoniger; 18 – A. pallipes; 19 – C. pilosa; 20 – B. depilis; 21 – S. impar; 22 – P. pennsylvanica; 23 – Myrmecina americana; 24 – S. ohioensis; 25 – A. rudis; 26 – S. molesta.

habitats, had estimated habitat diversities of 2.6–2.9, and can be considered habitat generalists. A third group is comprised of seven "intermediate" species (*L. ambiguus, L. curvispinosus, Myrmecina americana, S. ohioensis, Tapinoma sessile,* and *P. melanderi*). These showed habitat diversities of 1.6–2.2, and had significant numbers of occurrences in at least two habitats.

Three of the five habitat specialists were restricted to the mature forest site, and two were found only in the old-field. Although no species was limited to the young forest, four species were most abundant there. Most species specialized either on old-field habitat, or on forested habitats, and only 4 of 15 species had less than 95% of their occurrences in one or the other group.

Fig. 2 illustrates seasonal trends in the number of species, number of individual ants, number of species occurrences, and the species diversity per 10-sample collection. Overall ant activity in the litter zone is highest between May and October, but the timing and magnitude of maxima vary among habitats. Samples from the mature forest site tend to show the greatest abundance and diversity of ants in most months, but ephemeral activity peaks in late spring at the young forest site and in mid-summer at the old-field site equal or exceed the mature forest values for all variables except number of species occurrences (Fig. 2). The maximum number of species per 10 litter samples is the same (n = 14) at all three sites. Maximum species richness is attained in May at the young forest site, June at the mature forest site, and July at the old-field. Diversity peaks at the same time as total species number at the old-field and young forest sites, but at the mature forest site a fairly steady maximum diversity of 9.0–9.7 effective species is maintained from early June through late September.

Serial correlation analysis (Tab. 3) shows that month-to-month fluctuations in diversity, total number of species, and number of occurrences, are lowest at the mature forest site and about equally variable at the other two sites.

A single species (*P. melanderi*) comprised 26.2% of the 4711 individuals collected in the litter samples, and the three commonest species together accounted for 70.4%, 81.9%, and 49.1% of the individuals collected at Sites A, B, and C, respectively.

Litter ant species vary in the timing of their seasonal activity maxima. Activity may peak in early spring (e.g., *C. pilosa, S. impar*), late spring (e.g., *L. curvispinosus,*
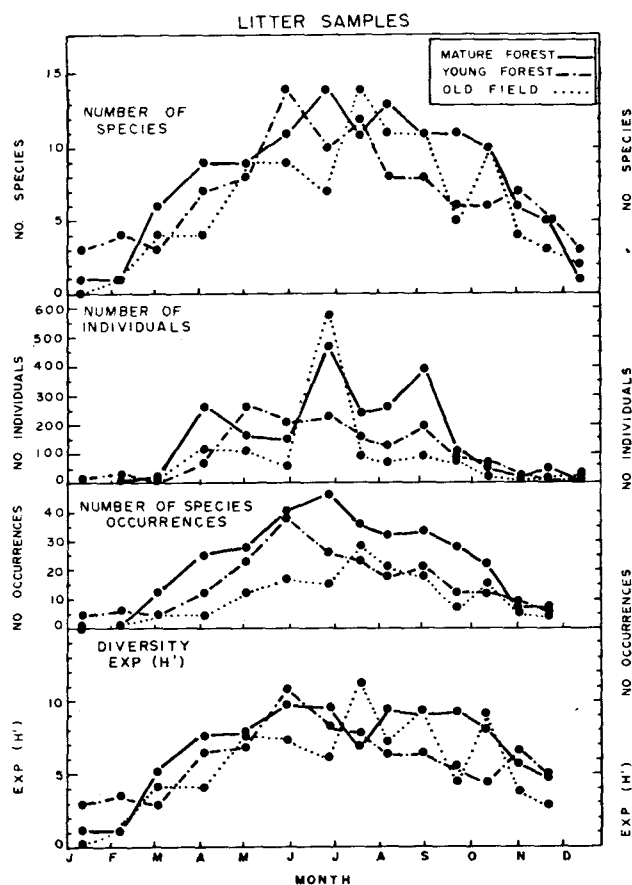

Fig. 2. Seasonal variation in the number of species, individuals, and species occurrences, and in the species diversity index for ants collected in the litter samples at three successional sites. Figures are based on 10 0.1 m² litter samples per site and sampling period.

L. alienus, Myrmecina americana), or early summer (e.g., *P. pennsylvanica, A. rudis*) (Figs 3, 4). Activity in the litter stratum is minimal between mid-November and late March.

3.1.3. The low arboreal fauna

The 510 samples, representing 25500 sweeps, yielded 7259 ants that belonged to 34 species (Tab. 1). The seventeen species that occurred in ten or more samples contributed 99.0% of the individuals and 96.1% of the species occurrences.

Tab. 3. Month-to-month stability in the number of species, individuals, species occurrences, and in the diversity index. Tabulated values are serial autocorrelation coefficients computed from successive samples. Fourteen pairs of litter samples and 16 pairs of sweep samples comprise the data.

Site	Description	Species		Individuals		Occurrences		EXP(H')	
		Litter	Sweep	Litter	Sweep	Litter	Sweep	Litter	Sweep
A	Old-field	0.66	0.77	0.26	0.37	0.73	0.72	0.59	0.70
B	Young Forest	0.62	0.66	0.69	0.22	0.72	0.71	0.62	0.66
C	Mature Forest	0.82	0.71	0.47	0.22	0.86	0.55	0.81	0.71

Tab. 4. Proportions of "large" collections of common litter ants that represented nest fragments, as judged by the presence of reproductives, brood, or callow workers. N_T = total number of occurrences; N_L = number of collections containing 5 or more conspecifics; N_R = number of nest occurrences.

Species	N_T	N_L	N_R	$\dfrac{100\times}{N_R/N_L}$ (%)
Ponera pennsylvanica	88	9	5	55.6
Aphaenogaster rudis	82	6	2	33.3
Paratrechima melanderi	82	13	10	76.9
Myrmecina americana	61	0	–	–
Leptothorax curvispinosus	59	11	7	63.6
Totals	372	39	24	61.5

Unlike the litter samples, the sweep samples show a very high correlation between the number of occurrences and the number of individuals of the 15 most frequent species ($r_s = 0.95$; $P < 0.01$). This reflects the fact that sweep samples are less likely to be dominated by highly localized aggregations of individuals. Moreover, because the litter stratum is a favored nesting horizon for many species that forage elsewhere, a disproportionately large number of litter samples contain sizeable nesting aggregations. This results in high levels of crowding and patchiness for most litter species (Tab. 2). In contrast, few local ant species nest in the thin stems and small twigs that are sampled by a sweep net, and mean crowding and patchiness statistics
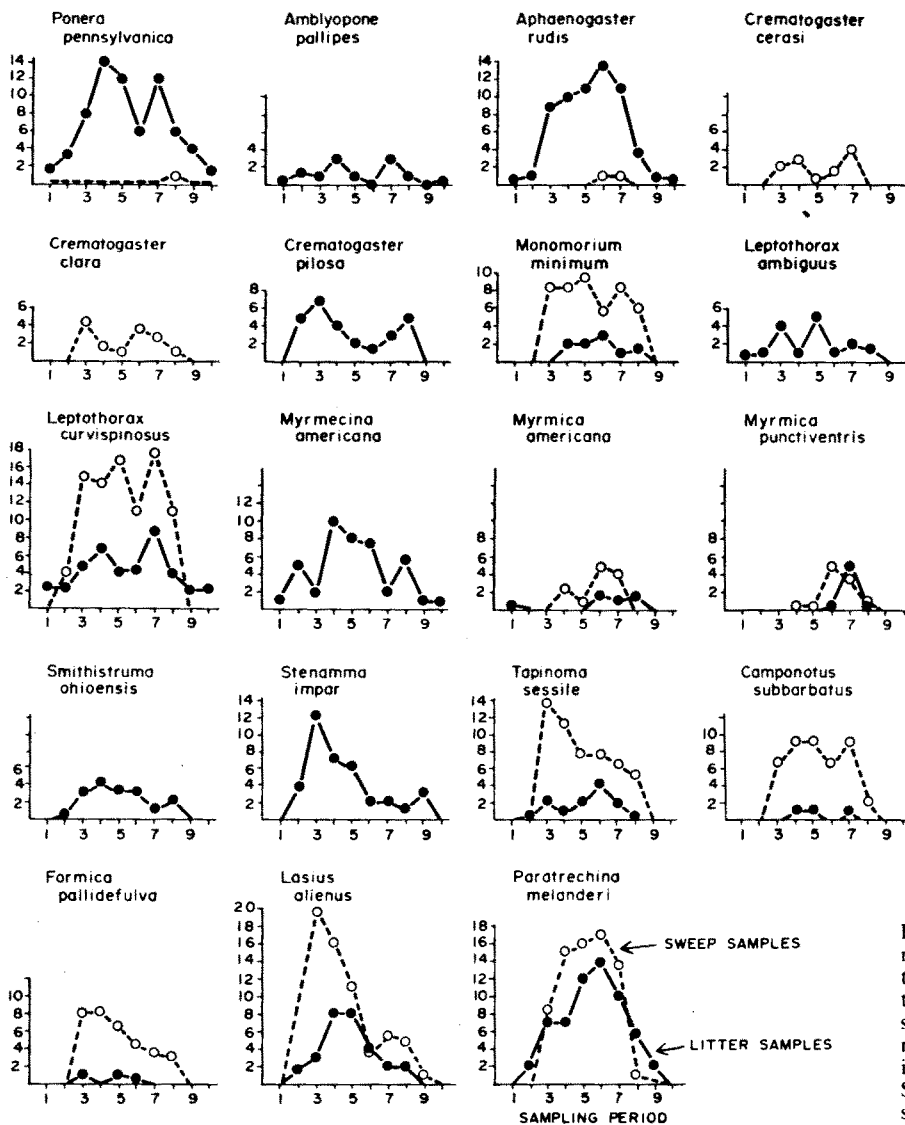

Fig. 3. Seasonal variation in the number of species occurrences of the 19 commonest ant species in the study area. Data for all three study sites are pooled, so maximum number of occurrences in a given sampling period = 30. See Tab. 4 for specification of sampling periods.

Fig. 4. Timing of seasonal maxima of the most abundant species (circled numbers) in relation to total community activity (solid lines) in old-field and forest ant communities, showing seasonal staggering of activity. Numerical species codes are given in legend to Fig. 1. Seasonal sampling periods specified in Tab. 5.
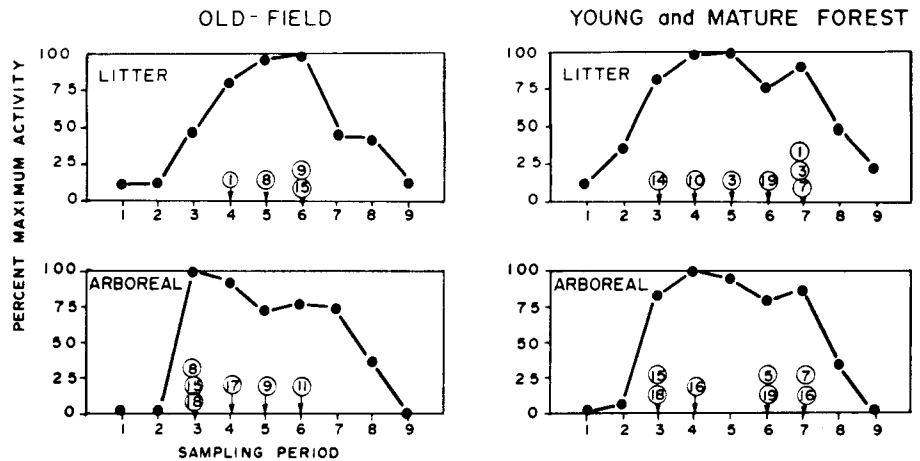
are substantially lower than in the litter samples. It should be emphasized that mean crowding for individuals (m^*) was computed per sample, not per unit area. Thus, the relatively low crowding values for the shrub-foraging component of the community imply a sparse distribution of ants in the shrub understory.

Habitat associations of arboreally foraging ants are summarized in a triangular diagram (Fig. 1). As in the litter zone, habitat specificity is relatively high and most species strongly differentiate between the old-field habitat and the two forested habitats as a group. There are, however, some differences in habitat specificity between arboreal and litter-foraging species. Three litter-foraging species were restricted to the mature forest site, but no arboreal species were so restricted. In addition, two species occurred relatively commonly in sweep samples from both the old-field and mature forest site, but were rare or absent in collections from the young forest site.

Different species dominate the litter zone and the low arboreal stratum. Eight of the twelve species that occurred most frequently in the litter samples were rare or absent in corresponding sweep samples. Only four species (*L. curvispinosus, T. sessile, L. alienus,* and *P. melanderi*) were abundant in both strata (Fig. 3). These four species frequently nest in the litter, but forage arboreally.

Fig. 5 summarizes seasonal changes in the number of species, number of individuals, number of species occurrences, and species diversity for the sweep samples. Indices of ant activity fluctuated more erratically in the sweep samples than in the litter samples at site C (mature forest), but not at the other two sites (Tab. 3). Ants in the shrub layer became active later in the spring and disappeared earlier in the autumn than did ants in the litter zone. Both total number of species and the effective number of species tended to be somewhat lower in the sweep samples than in the corresponding
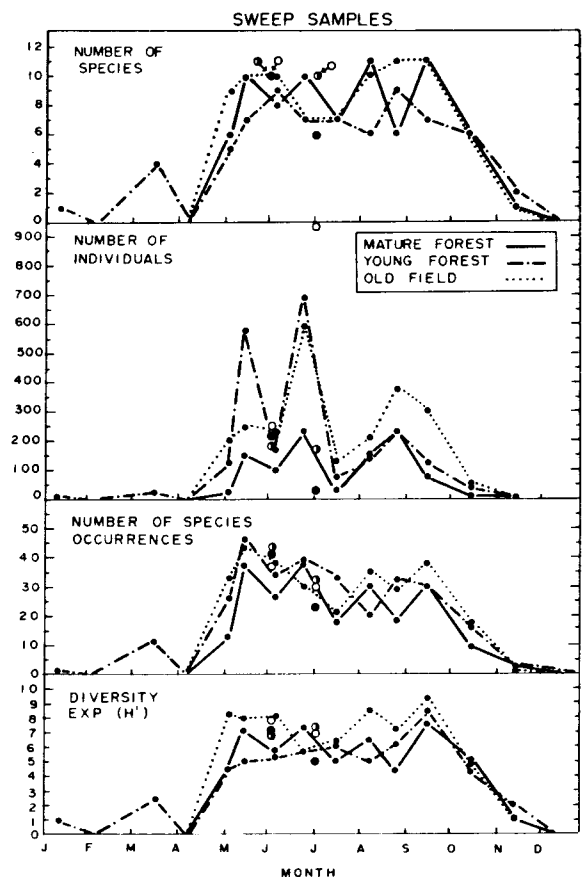

Fig. 5. Seasonal variation in the number of species, individuals, species occurrences, and in the species diversity index for ants collected in sweep samples at three successive sites. Plots are based on 10 50-sweep samples per site and sampling period. Circles not joined by lines represent "overlap" samples taken during the 13th and 14th months of the study (open circles – old-field; split circles – young forest; closed circles – mature forest).

litter samples, despite the much larger area of habitat included in the former. As noted above, this may be due to the fact that many species which nest in litter do not forage there, but could also reflect the relative inefficiency of sweep sampling. The number of individual ants per sweep sample showed a complex pattern of seasonal variation in the three habitats (Fig. 5). In general, the number of species occurrences reached a maximum between mid-May and early June, declined somewhat in mid-summer, then rebounded in late August or mid-September, before declining sharply in October. Species diversity followed a similar overall pattern at all sites (Fig. 5), and all three sites showed a major diversity peak in September. This contrasts with the pattern seen in the litter samples, where diversity was highest in late spring (two forested sites) or mid-summer (old-field site).

A few common species numerically dominated the sweep samples. *Leptothorax curvispinosus* and *Paratrechina melanderi* together accounted for 71.4% of the 3666 ants sampled from the two forested sites, while *Monomorium minimum* alone comprised 70.9% of the 3593 ants in the old-field sweep samples. The three commonest species in each habitat together accounted for 83.9% (mature forest), 80.1% (young forest) and 87.7% (old-field) of the individuals collected. *L. curvispinosus* showed strong activity peaks in mid-May and late June, with a somewhat weaker maximum in late August. Other abundant species generally exhibited a bimodal pattern, with a spring early summer maximum and an August or September maximum, separated by a mid-summer hiatus. Abundant sympatric species tended to have different seasonal maxima (Fig. 4). Of the common forest species, *L. alienus* peaked in mid-May, *L. curvispinosus* in mid-May and late June, and *P. melanderi* in late June. In the old-field habitat, *T. sessile* exhibited maximum annual activity in mid-May, *F. pallidefulva* in late June, and *M. minimum* in early July. The similarity of the samples taken 5 June 1975 and 3 June 1976 suggests that seasonal patterns may be relatively stable.

3.2. Components of diversity

The results to this point indicate that major habitat segregation, vertical stratification, and seasonal displacement of activity all differentiate ant species in the study area. However, a formal analysis of diversity components is necessary if the relative importance of the individual components and their interactions are to be evaluated. The three habitats (i's), two vertical strata (j's), and nine seasonal time intervals (k's) gave 54 resource states for which diversity indices (D_{ijk}'s) were calculated.

Tab. 5 gives the main results of the diversity analysis, which can be summarized as follows: The total diversity of the collection, over all habitats, vertical strata, and seasons, is 15.0 equally abundant species. About 37% of the total diversity is contributed by overlap of species within the same resource states, i.e., by co-occurrence at the same time of year in a particular habitat and microhabitat. This can be termed the "within micro-habitat" component of diversity.

Among-habitat differences (i.e., habitat specialization) account for 22% of the total diversity, vertical segregation (i.e., microhabitat specialization) contributes 16%, and seasonal staggering of activity patterns accounts for 12%. Thus, spatial and temporal segregation together contribute about half of the total community diversity. The remaining 13% of the observed diversity is due to two-way and three-way interactions between seasonal time, microhabitat, and major habitat, the most important term being a positive two-way interaction between major habitat and vertical microhabitat ($R_{AxB/C}$). This reflects the fact thay there is a degree of redundancy in the information given by successional, habitat and vertical stratum, i.e., that these two niche axes are not independent.
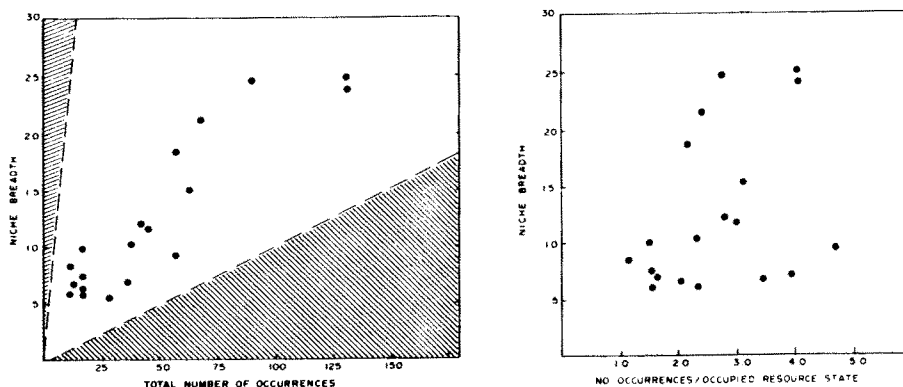

Fig. 6. A. Correlation between multidimensional niche breadth and total number of species occurrences for the 19 commonest ant species. Combinations within the cross-hatched areas are not possible. B. Multidimensional niche breadth as a function of the density of ant species in the habitats where they occur. The correlation in A is eliminated, showing that local abundance ("crowding") is largely independent of niche breadth.

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Tab. 5. Results of Analysis of Diversity Components. Niche dimensions are major habitat type (i's), vertical microhabitat (j's), and seasonal interval (k's). See text for definitions. Analysis follows methodology of Alatalo and Alatalo (1977).

I. Major habitat type (A)

	Successional Habitat (i's)			
	Mature forest (i=1)	Young forest (i=2)	Old-field (i=3)	
$\bar{D}_{i..}$	6.67	6.16	5.48	Weighted mean diversity
$D_{i..}$	9.40	8.96	8.44	pooled diversity

II. Vertical microhabitat (B)

		Vertical stratum		
	Litter (j=1)	Arboreal (j=2)		
$\bar{D}_{.j.}$	7.18	5.17	weighted mean diversity	
$D_{.j.}$	13.35	9.74	pooled diversity	

III. Seasonal interval (C)

	L.Nov– L.Feb (k=1)	E.Mar– E.Apr (k=2)	M.Apr– M.May (k=3)	L.May– M.Jun (k=4)	L.Jun– E.Jul (k=5)	M.Jul– E.Aug (k=6)	M.Aug– M.Sept (k=7)	L.Sept– M.Oct (k=8)	L.Oct– M.Nov (k=9)	
$\bar{D}_{..k}$	3.89	6.21	6.04	6.32	6.25	6.53	6.51	5.44	3.89	weighted mean diversity
$D_{..k}$	8.41	9.44	13.86	14.26	12.88	13.28	13.68	13.90	6.11	pooled diversity

Diversity due to independent contributions of A, B, and C:

$V_{A/BC} = 3.13$ $V_{B/AC} = 2.25$ $V_{C/AB} = 1.57$

Diversity due to 2-way interactions between A and B, A and C, B and C:

$R_{AxB/C} = 1.87$ $R_{AxC/B} = 0.68$ $R_{BxC/A} = -0.98$

Diversity due to 3-way interaction between A, B, and C:

$R_{AxBxC} = 0.24$

Percent importance of:

Major successional habitat alone $= (100 \times V_{A/BC})/(D_{...}-1) = $ 22.5%
Vertical segregation alone $= (100 \times V_{B/AC})/(D_{...}-1) = $ 16.1%
Seasonal non-overlap alone $= (100 \times V_{C/AB})/(D_{...}-1) = $ 11.3%

Subtotal 49.9%

Overlap between species in same resource state $= 100 \ (\bar{D}_{...}-1)/(C_{...}-1) = $ 37.2%
Two-way interactions $= 100(R_{AxB/C} + R_{AxcC/B} + R_{BxC/A})/(D_{...}-1) = $ 11.3%
Three-way interactions $= (100 \ R_{AxBxC})/(D_{...}-1) = $ 1.7%

Grand Total 100.1%

It is worth emphasizing that the relative importance of these three major niche dimensions could change (perhaps dramatically) if additional resource states or dimensions were included in the analysis. For example, vertical segregation might become more important if the soil zone and the high arboreal stratum were sampled in addition to the litter and shrub layers.

3.3. Niche breadths of individual species

Fig. 6 (left) summarizes the relationship between niche breadth and overall abundance for the 19 commonest species. As found by Levins (1968) for *Drosophila*, more abundant species tended to have broader niches, but considerable scatter is evident. For example, *Monomorium minimum* had a slightly narrower niche

than *Smithistruma ohioensis,* although the latter species was encountered only about a third as frequently. Conversely, *M. minimum* and *Tapinoma sessile* occurred with equal frequency (mean annual number of occurrences = 56.5 and 56.9, respectively), but *T. sessile* had about twice the computed niche breadth of *M. minimum* (18.4 vs. 9.2).

The partial independence of niche breadth and abundance is evident from the fact that the correlation between the two virtually disappears if niche breadth is plotted against mean density per occurrence, a measure of the local abundance ("crowding") of species where they occur (Fig. 6 right). Species with very low numbers of individuals per occurrence still tend to have narrow computed niches, but locally abundant species may be either broad-niched (e.g., *Paratrechina melanderi, Leptothorax curvispinosus*) or specialized (e.g., *Formica pallidefulva, M. minimum*).

4. Discussion

4.1. Ecological specialization in the ant community

Even the common ant species in the study area tend to be relatively specialized with respect to successional habitat or vertical stratum, or both. This can be appreciated if species occurrences are plotted on a square diagram, the corners of which represent the four possible specializations on habitat and microhabitat (Fig. 7). No fewer than 13 of 19 species plot in one of the four corner sectors of the graph, and no species fall within the "extreme generalist" sector at the center of the figure. The most common habitat-microhabitat specialization is "forest/terrestrial" (6 species), followed by "old-field/arboreal" (4 species) and "forest/arboreal" (3 species). There are no "old-field/terrestrial" specialists, probably a reflection of the sparsely developed, poorly buffered litter zone that characterized the old-field site. Most ants that do forage in the old-field litter layer nest elsewhere, usually in the soil. Extensive baiting surveys (Lynch unpubl.) indicate a high density of surface-foraging ants, as opposed to litter-foraging forms, at site A.

There is a sharp discontinuity between the seven ant species that rarely or never forage arboreally and the 12 species for which arboreal occurrences accounted for a high proportion (40–100%) of the collections. A similar arboreal-terrestrial polarization has been noted for Caribbean ants (Levins et al. 1973). Although arboreal nests were uncommon at any of the three study sites, arboreally foraging workers were common in all habitats. Species identities generally differed between the old-field site and the two forested sites, and only one terrestrial species (*P. pennsylvanica*) and two partly arboreal forms (*P. melanderi* and *L. alienus*) occurred regularly in forested and unforested habitats.

Ant species that commonly co-occur in a given habitat and microhabitat tend to differ in their adapta-
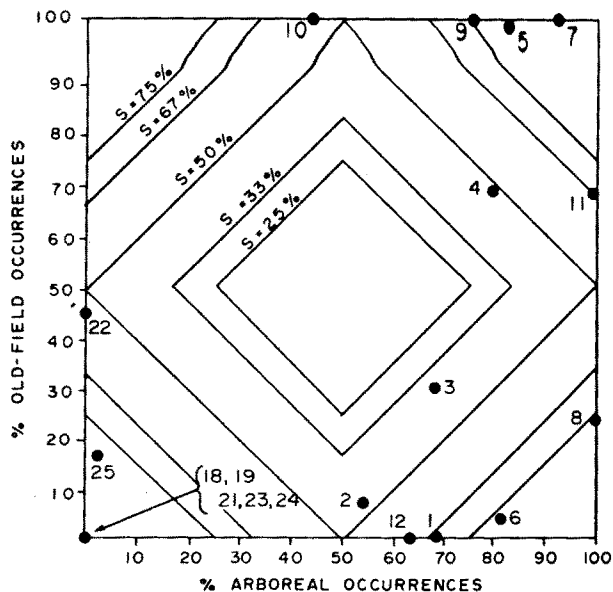

Fig. 7. Habitat-microhabitat specialization in the 19 commonest ant species. The corners of the diagram represent the four possible double modes of specialization: forest/litter (lower left), forest/arboreal (lower right), old-field/litter (upper left), and old-field/arboreal (upper right). Habitat-microhabitat generalists would plot toward the center of the diagram, but no such species exist among the group studied. Concentric square contours are lines of equal specialization (S), where S = abs (% old-field occurrences − 50) + abs (% arboreal occurrences − 50). Note that most species are highly specialized (S > 75%).

tions for finding, handling, and defending food (Lynch et al. 1980). A few of the litter species encountered in the present study are highly specialized hunters of particular arthropod prey. Thus, *Amblyopone pallipes* feeds primarily on soil centipedes, while *Smithistruma ohioensis* and its several congeners are predators on Collembola (Creighton 1950). This sort of dietary specialization is, however, the exception among temperate zone ants, most of which are rather generalized scavengers of dead or immobilized invertebrates and carbohydrate-rich solutions produced by plants (Carroll and Janzen 1973, Stradling 1978). Within these broad limits, there is ample room for the evolution of morphological and behavioral adaptations associated with particular feeding patterns, and temperate zone ant communities are not structured solely by interspecific interference competition, though aggressiveness surely plays an important role. Factors such as body size, mandibular morphology, and foraging tactics will tend to result in feeding differences in microsympatric species even in the absence of aggressive interactions (Davidson 1977, Lynch et al. 1980).

4.2. Causes and effects of interspecific differences in seasonal activity

An earlier study of surface-foraging ants at the mature forest site concluded that the commonest species (*Pre-*

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nolepis imparis) effectively avoided substantial annual overlap with potential competitors by foraging at low temperatures in spring and autumn and by ceasing surface activity during the warm mid-summer period when other species are abundant (Lynch et al. 1980). The major litter and arboreal species do not show the same extreme degree of seasonal segregation, but interspecific differences are evident (Figs 3, 4). Three basic patterns of seasonality can be distinguished: (a) bimodal asymmetrical – a major spring or summer peak separated from a lesser autumn peak by a mid-summer hiatus (e.g., *P. pennsylvanica, A. pallipes, C. cerasi, C. clara, C. pilosa, L. curvispinosus*); (b) unimodal symmetrical-a summer maximum with reduced activity in spring and autumn (e.g., *Aphaenogaster rudis, Myrmecina americana, Myrmica americana, M. punctiventris, Camponotus subbarbatus, P. melanderi);* and (c) unimodal skewed – a strong spring peak followed by a gradual decline in activity throughout summer and autumn (e.g., *Stenamma impar, T. sessile, L. alienus*). As noted earlier (see Fig. 4) the result of the diversity of seasonal activity modes in the local ant community is that annual activity maxima for the various species tend to occur in different months. Whitford (1978) documented a similar diversity of seasonal patterns in a community of southwestern U.S. desert ants.

The ultimate selective basis for interspecific differences in seasonality is unknown, but physiological differentiation is undoubtedly a proximate cause for some of the observed staggering of species. Thus, *P. imparis* has a lower Critical Thermal Maximum (CTM) than sympatric ant species that forage at higher temperatures (Tremper 1975, Lynch et al. 1980). Similarly, species that are primarily associated with old-field or other open habitats have been shown to be more tolerant of elevated temperatures than are forest-dwelling species from the same geographic region (Talbot 1934, Pressick 1972, Levins et al. 1973, Tremper 1975), and the same is true for species in the present study area (S. Vail unpubl.). Differences in CTM have been documented for sympatric ant species in deserts (Schumaker and Whitford 1974, Whitford and Ettershank 1975, Whitford 1978) and on tropical islands (Levins et al. 1973, Pressick 1972). The general conclusion has been that such differences may help allow coexistence by dispersing species through time or space, or both. The overriding importance of temperature as a factor controlling seasonal activity is emphasized by Markin et al. (1974), who found that geographic variation in the seasonal activity and reproductive performance of the imported fire ant (*Solenopsis invicta*) was almost entirely a function of temperature. Sanders (1972) reached a similar conclusion in his study of seasonal changes in the diel activity schedule of *Camponotus* spp. in southern Canada. Lynch et al. (1980) showed that temperature factors accounted for most seasonal changes in peak activity by the four commonest surface-foraging ant species at site C, but season (indepen-
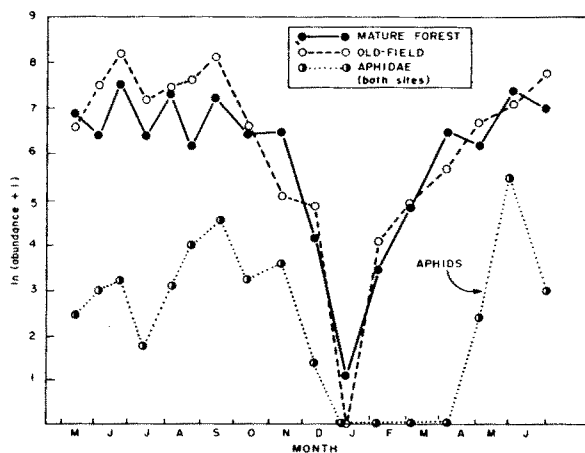

Fig. 8. Annual variation in the abundance of all understory arthropods and Aphidae at Sites A (old-field) and C (mature forest), based on the number of individuals per 500 sweeps at each site.

dent of temperature) had an added significant effect in two of the four species.

Whether or not competition among ant species has promoted species-specific seasonal activity modes, the overall seasonal pattern of community activity presumably reflects changes in the availability of food. A year-round sweep-sampling study of arthropod diversity and abundance at the mature forest and old-field sites (J. F. Lynch and W. G. Steiner unpubl.) indicated that the availability of arthropod prey and honeydew-producing Aphidae declined somewhat during mid-summer (Fig. 8), a period of reduced activity for many ant species.

Local ant species are known to exhibit seasonal shifts in their diel activity (Lynch et al. 1980), and a similar pattern has been shown for desert ants (Whitford and Ettershank 1975, Whitford et al. 1976, Whitford 1978). Such shifts may be direct responses to changing physical conditions, particularly temperature (Sanders 1972), but food availability and interspecific interference also may be involved (Pressick 1972, Levins et al. 1973, Whitford and Ettershank 1975, Whitford 1978). Controlled field experiments now in progress should help clarify the role of competition in determining diel activity patterns, but a complex combination of proximate and ultimate causal factors undoubtedly underlies observed patterns of seasonality in ants.

4.3. Patterns of dominance

Although 59 species of ants have been identified within the 1 km² area containing the three study sites, many are rare or local, or both. Most local species assemblages are numerically dominated by only a few species, particularly if only a given vertical stratum is considered. Thus, three species comprise 65% of the occurrences in sweep samples from the mature forest

site, 58% in corresponding samples from the young forest site, and 56% in samples from the old-field site. These percentages are even higher if dominance is computed on the basis of individual ants rather than species occurrences. In the litter samples, the three most abundant species contribute a somewhat lower percentage (35–53%) of the total occurrences. Levins et al. (1973) found a similar pattern of dominance by a few species in a study of Caribbean island ants, as did Culver (1974) in his study of ant communities in Puerto Rico and West Virginia.

Caution must be exercised when comparing the results of surveys conducted in different habitats or by different methodologies. As an example, Culver (1974) sampled surface and litter-foraging ants in West Virginia and the Caribbean using different combinations of baiting and litter extraction techniques. Results from these disparate sampling methods were combined in some of the analyses (e.g., niche breadth comparisons). Baiting and litter samples gave very different results in the present study area, and the same was presumably true for the sites studies by Culver. The problem is compounded by the fact that Culver (1974) based his estimates of resource removal rates (hence, competition) on the premise that all aggregations of five or more ants in litter samples represented feeding mobilizations. However, over 60% of such aggregations encountered in the present study were in fact nest fragments, as evidenced by the presence of reproductives, brood, or callow workers (Tab. 4). Much more information is required before we can determine whether or not tropical-temperate or grassland-forest gradients in community structure and competitive relationships among ants actually exist.

4.4. Components of diversity: comparisons with other studies

Comparison of the results of the present analysis of diversity components with previous studies is difficult because other workers have employed different sampling methods, considered different resource axis and states, used noninteractive hierarchical modes of analysis, and employed H′ rather than EXP(H′) as a diversity statistic. This latter difficulty may not seriously distort the results in all cases, but Alatalo and Alatalo (1977) have shown that H′ does not have the same additive properties as EXP(H′) in analyses of the present type. Despite these difficulties, cautious comparisons of results may be enlightening.

Previous studies of diversity components in terrestrial insect communities concern temperate-zone and tropical *Drosophila* (Levins 1968, Shorrocks 1975) and ants (Pressick 1972, Levins et al. 1973, Pressick and Herbst 1973, Culver 1974, Feener 1978). Feener's study was conducted near Austin, Texas. Culver computed diversity components for ant communities in West Virginia and Puerto Rico. The three remaining ant references all

concern the same study conducted on St. John, Virgin Islands.

Levins (1968) compared the relative contributions of seasonality, habitat, and within-habitat overlap to total diversity for *Drosophila* communities in Texas, Puerto Rico, and Brazil. His main conclusion was that seasonality became an increasingly important determinant of diversity with increasing latitude; thus, the seasonal component of diversity accounted for only 3% of the total community diversity at Belem, Brazil, but increased to 29% in the vicinity of Austin, Texas.

The results of Shorrock's (1975) study of English *Drosophila* are consistent with Levins' conclusions: seasonality accounted for 36% of the observed community diversity, while vertical segregation, within microhabitat overlap, bait type, and habitat (= "horizontal") segregation were successively less important. If the contributions of bait type and within-bait diversity are combined into a single "within vertical microhabitat" component, season, habitat, vertical microhabitat, and within-microhabitat overlap respectively contribute 36%, 9%, 21%, and 30% of the total community, diversity. This can be compared with figures for the present ant study: season − 12%; habitat − 22%; vertical microhabitat − 16%; overlap − 37%. Aside from the greater importance of seasonal differences in the English fruit fly community, the major difference in the results of the two diversity analyses is the surprisingly low importance of habitat differentiation in the latter. Shorrocks (1975) also remarked on this seeming anomaly, but the different results of the two studies may simply reflect the fact that the five habitats sampled by Shorrocks were all wooded areas, whereas the present study considered old-field habitat as well as two types of forest.

The paper by Pressick and Herbst (1973) summarizes the diversity analysis for the St. John, Virgin Islands, ant community (see also Pressick 1972, Levins et al. 1973). Pressick and Herbst sampled eight diverse habitats, including sandy beach, grassy field, scrub, and various forest and woodland types. The four microhabitats considered in their study were nesting sites rather than foraging areas, but both arboreal sites (twigs) and terrestrial sites (ground, rocks, logs) were sampled, thereby making possible at least a first-order comparison with the results of sweep samples and litter samples. A final difference in the approach of Pressick and Herbst and that employed in the present study is that the former authors did not study seasonal variation in community composition.

Pressick and Herbst (1973) found that habitat differences contributed the highest proportion (39%) to the total community diversity, but overlap within microhabitats was nearly as important (35%). Between-microhabitat (i.e., nest site) differences accounted for a lesser percentage (26%) of the total. For the present study, if seasonality is omitted for the sake of comparison, the equivalent figures are: habitat − 25%; with-

in-microhabitat overlap – 42%; between-microhabitat (vertical sites) – 18%.

Culver's (1974) comparison of diversity components in West Virginia and Puerto Rican ant communities is based on analysis of litter samples from second growth woodlands in both areas. Seasonal turnover of species and vertical stratification were not considered, and Culver's "between-site" comparisons involved samples taken 5 m apart within the same patch of woodland. No relevant comparisons can be made on the bases of these data at this time, although variation between litter sampling stations at a given site (e.g., the young forest area) could be compared if my data were re-arranged.

Feener (1978) studied ants in a single habitat (oak-hackberry woodland), and vertical stratum (litter zone) near Austin, Texas. Sampling was conducted only in the warm-weather months (May–November) but this period probably encompassed the major activity periods of most or all species. Feener found that seasonality contributed only a small proportion of observed local diversity (average approximately 8%); variation among and within sampling sites accounted for the remaining 92% of the observed community diversity ($H' = 2.1 =$ 7.9 equally abundant species). When the effects of major habitat and vertical segregation are removed from the present study, the effective number of ant species in the community drops from 15.0 to 7.3, a figure closely comparable to that for the Texas oak-hackberry woodland. However, in the Maryland ant community, seasonal differentiation contributes 25% of the residual diversity, vs. 8% for the Texas community.

Thus, the fragmentary existing data for ants and fruit flies support Levins (1968) contention that seasonality makes a more important contribution to community diversity in temperate than in tropical communities. That this finding may not be universally valid for insects is suggested by growing evidence for marked seasonality in light-trap samples of many tropical insects, particularly in areas with a well-defined dry season (Wolda 1977, 1978a,b, 1979).

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